XVI.—On the Representative Relationships of the Fixed and Free Tunicata, regarded as two Subclasses of equivalent value; with some General Remarks on their Morphology. By John Denis Macdonald, R.N., F.R.S, Surgeon of H.M.S. "Icarus." Communicated by Professor Maclagan. (Plate IX.)

(Read 15th December 1862.)

My first precise views of the structure of the Tunicata were formed by the perusal of Mr Huxley's masterly papers dealing with the anatomy of Salpa, Pyrosoma, Doliolum, and Appendicularia, in the Phil. Trans. for 1851, Part II.; and I have since had abundant opportunity of verifying all the important facts, made known by that original observer, in the papers to which I have alluded.

Having thus acknowledged my guide in this field of research, I can scarcely claim much originality as relates to pure anatomy; but I hope that the method here adopted, in opening up this interesting subject, will be found in keeping with nature, as it is the result of much study and practical investigation.

I must first beg the question, and next endeavour to support it, that the class *Tunicata* may be conveniently divided into two subclasses—viz., the fixed or stationary, and the free or locomotive. The latter, from their habit of life, are also commonly denominated *Pelagic*; while the former, by general consent, chiefly following the suggestions of M. Milne-Edwards, have been divided into the *Simple*, the *Social*, and the *Compound*, as given in the following table:—

Tunicata.

1. Fixed or stationary.			
1. Solitary, or simply segregate.			
a. Sessile (recumbent or erect), or pedunculate,			Simple.
2. Organically blended in communities.			
a. Sessile or pedunculated on a common axis,			Social.
b. Immersed in a common test substance,			Compound

Of the fixed Tunicata, it would appear that *Pelonaia* and *Chelyosoma** present characters which at once distinguish them from all the other members of the subclass. Thus, in the genera named, the branchial membrane seems to be closely adherent to the subjacent textures, without forming a distinct sac.

Pelagic.

II. Free or locomotive,

^{*} We are much in want of more accurate information respecting these genera. Mr Huxley remarks, loc. cit. 588, "In Pelonaia, the hypopharyngeal band has disappeared. It is a Salpa in which the oral and cloacal orifices have approximated, while the 'gill' has become obliterated;" and in a note at the bottom of the page he says, "Chelyosoma would appear to resemble Pelonaia in the absence of any distinct branchial sac; but Eschricht's figures are not very clear."

though finely areolated and thrown into parallel folds; whereas, in all the remaining fixed Tunicata, a branchial sac may be demonstrated, the respiratory slits or meshes being in general longitudinal, and disposed in many transverse series. On the other hand, the respiratory system in the free or Pelagic section presents no less than four distinct types, as occurring respectively in the genera Pyrosoma, Doliolum, Salpa, and Appendicularia. These may be defined as follows:—

Branchial membrane sac-like, with transverse slits in single longitudinal series, strengthened by longitudinal non-ciliated bars. Apertures terminal or subterminal—Pyrosoma.

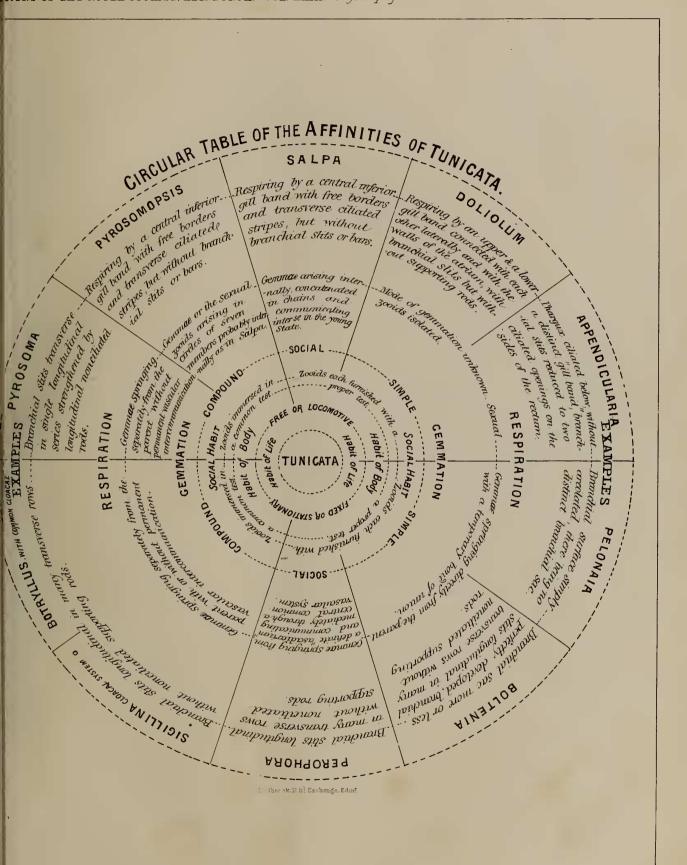
Respiring by an upper and a lower "gill-band," connected with each other laterally, and with the walls of the atrium; having branchial slits, but no supporting longitudinal bars. Apertures terminal—Doliolum.

Respiring by a central inferior gill-band, with free borders and transverse ciliated stripes, but without slits or bars. Apertures terminal or subterminal—Salpa, &c.

Pharynx ciliated below without a distinct "gill-band;" branchial slits reduced to two ciliated openings on the sides of the rectum. Apertures approximated hæmally—Appendicularia.

As far as the respiratory system is concerned, therefore, the fixed Tunicata exhibit at least two well-marked types, and the Pelagic group four, which are equally distinct, and, as I conceive, of equal importance, demanding fair consideration in systematic arrangement. Moreover, I am quite satisfied that there are very striking representative relationships existing between the fixed and free Tunicata; and in order to exhibit these the more clearly, I have drawn up the annexed circular scheme or table, in which it will be seen that each subclass has its simple, social, and compound groups, and their mutual representatives may be at once recognised. Thus, Appendicularia represents the equally curious genus Pelonaia, Doliolum the remaining simple Tunicata, Salpa the social, and Pyrosoma, the compound group, but, in particular, the Botryllians. Any one accustomed to draw comparisons and analogies will readily perceive that there is something more than simple coincidence in all this, particularly as the characters employed are so comprehensive, bearing successively on habit of life, habit of body, social habit, mode of gemmation, and respiration. It would be quite as easy to draw up two circles as one, or the characters might be thrown into rays instead of circles, but the result in all cases would be virtually the same.

I always pay respect to the maxim, that "characters can only be taken as natural when they have been proved to be so;" and I know also that groups must be found, before trustworthy characters can be chosen to effect a classification. When we find *Nerites* breathing air, and feeding on the green leaves of the





forest, Nerites breathing in the mountain streams, Nerites in brackish waters, Nerites on the beach in fellowship with Littorina, and in the sea itself, one would say that habit of life would afford anything but a natural character. Nor indeed would it in the case given, and in many others that might be adduced; but it certainly affords us the simplest and most natural primary division of Tunicata, and the other characters adopted in the table appear to answer their purpose equally well.

The idea has been too commonly entertained, that the Pelagic Tunicata, so called, compose a group only commensurate with the compound, the social, or the simple, taken separately, but I trust that a candid analysis of the preceding table will serve to free the judgment from an accustomed bias in this particular, and show that the fixed and the free Tunicata form two subclasses of at least nearly equal value in a zoological point of view; and I almost imagine, though myself affected by the prejudice to which I have alluded, that the balance is rather in favour of the Pelagians.

Though we may readily, as by a kind of empiricism, recognise a difference between the *simple*, *social*, and *compound Tunicata*, it is by no means easy to give them an intelligible definition. Indeed, I can safely say, as a student of the Tunicata, that I have long known more of the existence of a difference than of its precise nature, and this can scarcely be arrived at by the study of books alone. Indeed, the whole subject is even now shadowy and ill defined, notwithstanding the great light that has been shed upon it by the labours of Savigny, Macleay, Fleming, Milne-Edwards, and, in particular, Professor Huxley.

The term Compound is just as applicable to a tree of *Perophora*, as it is to one of *Sertularia*; but that term is restricted to another group, including forms that differ remarkably *inter se*, such as *Botryllus* and *Sigillina*, for example, their great characteristic being, as far as I can see, more or less complete immersion of the zooids in a common test, with or without vascular intercommunication. This immersion of the zooids is an important feature, as no common cloacal system can otherwise exist; but, inasmuch as it may occur without the formation of cloacæ, it links the *social* group with such compound Tunicaries as possess a common cloacal system. Furthermore, the branched and undermining form of this system, in several genera, indicates the passage to the Botryllian punctate, linear, or reticulate type, in connection with which latter, as a genetic character, several zooids are developed from a single ovum, as in *Pyrosoma*.

The process of gemmation, on the other hand, is much more energetic in the social than in either the simple or compound Ascidians. Thus, we scarcely ever find incipient buds springing from, or beyond others little farther advanced in the two latter, while such is the rule in the former group.

That the increase of the connecting substance, or "ascidiarium" of Huxley, proceeds pari passu with the gemmæ, and is, in fact, in advance of them in the

social Ascidians, as in the *Polyzoa*, can scarcely be denied; and upon it is impressed a limited law of growth or extension which is subservient to the forces determining the development of the zooids. Thus, while both progress in harmony, there are obvious indications of the co-existence of independent powers.

The primary fixed point, or, as it were, the potential germ of the ascidiarium, taken in the abstract, will be found to be very differently related to the zooids in the compound as compared with the social Ascidians. Thus, the point of attachment of a Perophora or Chondrostachys, for example, may be looked upon as homologous with the cloacal side of the apex, so called, in Pyrosoma, Plate IX. fig. 1 a', or to the corresponding part in Botryllus, Plate IX. fig. 2 a', the attached surface of the latter genus, Plate IX. fig. 2 a, being equivalent to the exterior side of the apex in the free Pyrosoma, and to the summit of the axis, produced in Chondrostachys, Plate IX. fig. 1 a, and depressed in Diazona, which latter genus appears to me to be more conformable with the social than with the compound group. The hæmal surface of the zooids, we therefore find, is turned in opposite directions in *Chondrostachys* and *Botryllus*,—viz., in the former case, towards the summit of the growing axis, and, in the latter, towards the margin of the encrusting common test, or, in other words, the zooids face outwards in one instance and inwards in the other. Though all the gemme augmenting the community are dorsal in both examples given, yet, in Botryllus, and especially in Pyrosoma, they are being continually thrown forward, so as ultimately to be in advance of the parent zooids, whereas in the social group, the anterior aspect of the primary zooid being turned towards the surface, upon which the rudimentary ascidiarium is fixed, the new gemmæ arise within extensions of the connecting substance in a truly retrograde direction,—i.e., centripetally, or towards the summit of the central axis thus formed.

In the beautiful species of *Botrylloides*, of which there are many in the Australian seas, I have frequently observed a rear-rank of gemmæ advancing to usurp the place of their parents, which had for some time previously played their part at the fore; and indeed it is only in this way that the linear and reticulate cloacæ (along the sides of which two rows of zooids are at most to be found), can be produced.

The bell-shaped antroversion of the "ascidiarium" in *Pyrosoma* appears to be necessitated by the position of the "cyathozooid," so accurately described by Professor Huxley, and of the cloacal apertures of the four "ascidiozooids" surrounding it, as also by the peculiar mode of advance of the gemmæ, and the forward extension of these palliovascular stolons, which are in all Tunicata intimately connected with the growth and nutrition of the test.

The proximal surface of *Botryllus*, being fixed, presents so great antroversion of the mass as happens in *Pyrosoma*, which, in consequence of being quite free,

admits of the full play of this tendency, aided by a more rapid development of the zooids. Moreover, it would appear, that the margin of the external opening of the common cloaca is permanent, progressively advancing with the newly formed zooids, thrusting themselves forwards between it and the parents from which they sprung. Whereas, in *Botryllus* or *Botrylloides*, where there is but one effective row of zooids bordering the cloacæ at any particular time, the margins of the openings must be continually undergoing repair and decay.

On comparing an expansion of *Botryllus* with one of *Flustra*, or any other polyzoon, it is curious to observe that the zooids lie virtually face downwards in the latter, and face upwards in the former; and this is certainly one amongst many points of difference existing between the *Polyzoa* and the *Compound Tunicata*, while it favours the view that the *Polyzoa* hold the same relationship to the *Brachiopoda** that the compound hold to the simple *Tunicata*, or, to extend the question, that a *Gorgonia* bears to an *Actinia*.

A test which is common to a number of individuals, i.e., an Ascidiarium, affords the first bond of union or community occurring in Tunicata. The next is obviously the establishment of a common cloacal system; and, lastly, as it would appear, the most important condition, truly suggesting the designation compound, is the intercommunication of the Pallio-vascular systems of the zooids, either as connected with the process of gemmation alone, or with the nutrition of the common test. Systems of intercommunicating stolons, having no connection whatever with gemmation, frequently present themselves in the compound genera; thus, in Leptoclinum and others, they are simple, or simply branched without reticulation; while, in Botryllus, they are compound, reticulate, and open a communication between the zooids.

The cloacal, like the branchial aperture, may open upon the external surface of the common test, or it may open into a definite common cloacal system either directly or by a tributary canal. The character and arrangement of the common cloacæ are of great importance in classification, and it is much to be regretted that so little definite information respecting them is to be found in systematic works. Whenever the opportunity presented itself, I have always endeavoured to unravel their curious schemes of arrangement, and often found it a matter of great difficulty; but so far as I have been able to generalize them, they are given in the following classification, which will be also found to afford a simple exposition of the leading features of the *Tunicata* as a whole.

As a matter of course, many characters in the minor distinctions here employed must, and have been, previously adopted by others. Thus, Mr W. S. M'Leay and Dr Fleming have passed in review nearly all the available characters in the Simple Tunicata, and M. Milne-Edwards has done the same with the

^{*} The ventral valve being the valve of attachment in the Brachiopoda as in the Polyzoa.

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social and compound groups. I hope, therefore, that this will be sufficient apology, without complicating the table by continual reference to authority.

CLASS TUNICATA.

Marine molluscoid animals, fixed or free, invested by an outer coat or tunic of variable consistency, and communicating with the exterior by an inhalent and an exhalent orifice for respiratory currents, conveying also the materials used as food; having a ciliated and variously modified pharynx adapted for respiration, and an atrial chamber for the discharge of the respired water and excretions, a reversible circulation, sexes combined, and the power also of developing by gemmation, which property pre-eminently distinguishes them from the mollusca proper.

SUB-CLASS I.

ANIMALS FIXED OR STATIONARY.

Branchial membrane closely adherent, or more or less perfectly sac-like, simple distinctly retiform; the meshes disposed in many transverse series without n	
porting bars.	
1. Gemmæ springing directly from the parent with a temporary bond	SIMPLE
of union,	TUNICATA.
A. Branchial membrane adherent, not forming a distinct sac. Ten-	Genera.
tacula, o. Branchial folds transverse,	Pelonaia.
B. Branchial membrane more or less perfectly sac-like.	
1. Tentacula o, (?)	Chelyosoma.
2. Tentacula simple, liver rudimentary, animal sessile (erect or re-	
cumbent).	
a. Branchial folds, o,	Ascidium.
b. Branchial folds longitudinal.	
1. Branchial aperture higher than the cloacal, .	Cynthia.
2. Apertures on the same plane.	
a. Protected by a D-shaped apercular fold of the	e
test common to both,	Peroides.
b. Simple or naked.	
1. Ovary and testis on right side,	Pandocia.
2. Ovary and testis on the left side, .	Dendrodoa.
3. Tentacula compound. Branchial folds numerous, longitudinal	,
liver well developed.	
a. Sessile (erect), apertures on the same plane,	Cæsira and
	Molgula?
b. Pedunculated (pendulous) cloacal opening, the higher of	r
subterminal,	Boltonia and
	Cystingea.

ABLE OF CLASSIFICATION—continued.
2. Gemmæ springing separately from a definite "ascidiarium (Hux.), and communicating
indirectly through a central common vascular system, . Social Tunicata.
A. Zooids branchial (Hux.), pedunculated, springing from a scandent or Genera.
repent corneous axis, with a central permanent vascular system .
common to the offsets,
B. Zooids intestinal (Hux.)
1. Pedunculated.
a Standing upon a repent ramose cartilaginous case, with a
central canal (usually not permanent), communicating with
the offsets,
b. Developed centripetally on an erect, simple, cylindrical stem,
permeated by numerous longitudinal canals communicating
with the offsets, though rarely with each other, Chondrostachys.
2. Sessile, clustered in irregular circles on a simple depressed axis, Syntethys.
And, probably, (?) Diazona.
3. Gemmæ arising separately from the parent, with or without vascular inter-
communication, but always immersed in a common test or "ascidi-
arium,"
A. Pallio-vascular system simple, i.e., not intercommunicating.
1. Excretory aperture opening directly upon the surface. Cloacæ o.
a. Biabdominal (Polyclinian). Zooids in irregular circles, one
above another, Sigillina.
b. Abdominal (Didemnian).
1. Zooids in one or two rows at unequal distances from
centres,
2. Zooids without distinct circumscription. a. Abdominal viscera beside the thorax, . Eucælium.
b. Abdomen pedunculate, Didemnium.
2. Excretory aperture opening into a common cloacal system.
a. Cloaca superficial reticulate, with tributary canals diverging
from the zooids in the intervening spaces. a. Thorax double,
b. Thorax simple, Leptoclinum.
b. Cloacæ deeply excavated, dendritic, formed by the con-
fluence of converging canals.
1. Biabdominal (Polyclinian).
a. Systems diffuse.
a. Branchial aperture 6-rayed, Amaræcium.
β. Branchial aperture 8-rayed, Parascidium.
b. Systems circumscribed.
. Without central cavities, Aplydium.
. With central cavities Polyclinum.

TABLE OF CLASSIFICATION—continued,

COMPOUND TUNICATA.

B. Palliovascular system intercommunicating.	Genera.
1. Excretory apertures opening directly into punctate, linear, or	
reticulate cloacæ.	
a. Biadominal (Polyclinian).	
1. Systems single, isolated, or gregarious in whole relief,	
pendunculated (?),	Synœcium.
2. Systems numerous, masses crusting.	
a. In half relief projecting above the surface, (?)	Sidnyum.
	Polychnoides.
b. Thoracic (Botryllian).	
	Botryllus.
	Botrylloides.
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SUB-CLASS II.	
ANIMALS FREE LOCOMOTIVE. PELA	GIC TUNICATA.
	Genera.
II. Branchial membrane, sac-like, with transverse slits in single longitudinal series,	
strengthened by longitudinal non-ciliated rods, apertures terminal or sub-	
	Pyrosoma.
III. Respiring by an upper and a lower gill-band, connected with each other laterally	
and with the walls of the atrium; having branchial slits, but no supporting	
longitudinal rods. Apertures terminal,	Doliolum.
IV. Respiring by a central and inferior gill-band with free borders, and transverse	
ciliated stripes, but without slits or rods. Apertures terminal or sub-terminal.	
1. Intestine short, and simply folded upon itself.	
A. Sexual zooids concatenated in chains.	
	Pegea.
2. Ciliated stripes of gill-band, simple,	Salpa.
B. Several zoids permanently united in circles, as in Pyrosoma,	
2. Intestine extended directly forwards from a cœcum-like proventriculus. The	
anus, and with it the ejaculatory duct, opening near the branchial orifice,	Orthocæta.
	Salpa pinnata.)
V. Pharynx ciliated below, without a distinct gill-band. Branchial slits reduced to	
two ciliated openings on the sides of the rectum. Apertures approximated	
$\it hæmally, \ldots \ldots \ldots \ldots$	Ippendicularia.
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The lobing, and other particulars connected with the apertures, afford simple and easily recognisable characters, which are often distinctive of genera; but, as the Table might be rendered too complex by their introduction, I have omitted them. They may, however, be readily supplied by the student for his own convenience. I have drawn up the preceding scheme of classification chiefly with the view of illustrating the principles set forth in the first part of the paper. My own doubts I have expressed with a query (?), and even independent of these

many errors may be patent to zoologists, better conversant with the Tunicata than myself. Such, indeed, can only be expected to occur in thus dealing with so comprehensive a subject. I believe, nevertheless, that our acquisitions, as well as those things which are yet desiderata in the interesting study before us, are made much plainer in an attempt of this kind, however imperfect, than perhaps in any other way. The following genera may require brief comment in reference to their zoological characters, and the position assigned to them in the Table:—

Chelyosoma.

The absence of branchial tentacula in this genus, and what has been already said of it, p. 171, suggests a position for it near *Pelonaia*.

Peroides (mihi).

Peroides is an Australian genus discovered by me on the Bellona reefs, lat. 21. 51. S., long. 159. 28. E., but as I have given an account of it, with figures, to the Linnean Society, I need only allude to its leading features, which are these,—animal recumbent on the left side; apertures simple on the same plane, and protected by a D-shaped operculum, composed of an indurated fold of the test common to both.

Cynthia, Cæsira and Molgula.

The term genus was received by the earlier zoologists in a much wider sense than that to which we now confine it; and, as might be expected, this has since given rise to much confusion, requiring considerable research to clear up satisfactorily. Thus, under the head of Cynthia, several distinct genera were included by Savigny, and we consequently find that the restricted genus, as understood by Professor Forbes, is represented as having a "circle of tentacular filaments," i.e., simple tentacula; whereas Dr Fleming gives Cynthia the character of "Tentacula compound," which could only be applied to a very different genus. It is also remarkable that without any reference to Professor Forbes's genus Molgula, in a paper read before the Linnean Society and published in the Transactions, I described two Australian Ascidians accurately conformable to Savigny's genus Cæsira, and which, singularly enough, very closely represent the two British species of Molgula described by Professor Forbes; and my impression has ever since been, that Cæsira and Molgula are synonyms of one and the same genus. Knowing, however, the great and respected authority which this view calls into question, I cannot be positive on the subject, but merely direct attention to it in the hope of setting it right.

Chondrostachys (mihi).

This name I have given to a very beautiful social Ascidian, which I first VOL. XXIII PART II.

dredged up in deep water in Bass Strait. The particulars of its anatomy, with several figures, were published in the Ann. and Mag. Nat. Hist. at the time; and it has since been obtained by Mr F. N. RAYNER, R.N., late surgeon of H.M.S. "Herald," in the neighbourhood of Torres Strait. It may be remarked, that the whole mass is quite colourless and pellucid, but in other respects it is sufficiently described in the table.

Diazona.

It has often appeared to me that *Diazona* was more closely related to the Social than to the Compound Tunicata, from the similarity of its structure to that of *Syntethys*. The position assigned to it in the table is quite in accordance with the definitions there given.

Diplosoma (mihi).

This genus I have found both in the S.W. Pacific and in the West Indies. The mass is gelatinous and filmy, and the thorax in the zooids is double—a condition that may be traced even long before the young escapes from the ovum. It was described and figured in the Transactions of the Linnean Society as the first step towards the still more paradoxical development of the ovum in Botryllus and Pyrosoma.

Synacium and Sidnyum.

Though certain general considerations have induced me to place these genera near the true *Botryllians*, I cannot yet say whether they have an inter-communicating palliovascular system or not; and as it would be equally wrong, should such be the case, to place them anywhere else, they may remain where they are until the question is settled, and the (?) is removed.

Polyclinoides (mihi).

I have applied this term to an Australian genus of compound Ascidians, distinguished from *Botryllus* by having a distinct abdomen, and the generative organs pedunculated, forming a post abdomen,—and from *Polyclinum*, by possessing a compound palliovascular system, and fewer zooids surrounding the cloacæ; besides which the mass is thin and encrusting, as in *Botryllus*. The branchial aperture is considerably elevated, and six-lobed. The superior margin of the cloacal opening is much produced, and three-lobed at the extremity, which is simple in *Botryllus*.

Pyrosomopsis (mihi).

A name which I have applied provisionally to a curious genus of Salpians, in

which the gemmæ are permanently united in circles, and thus described in my notes:—"This form presents seven perfect Salpians disposed in a circle, radiating, with their posterior extremities approximated near the centre, and enveloped in a common membrane, like a medusiform disc.

"Respiratory openings occupying one surface of the disc, the anterior or orifice of ingress being marginal, and the posterior central. The testis and a diverticulum of the alimentary canal forming two elongated papilliform processes, projecting from the posterior extremity of each animal (but within the common envelope), and convening towards the centre of the disc. Intestine forming an open arch, with its convexity directed backwards, across which the long and narrow duct of the testis passes to open into the respiratory chamber. Each zooid bearing a solitary embryo communicating with the sinus system, and enclosed in a spherical capsule.

- "Otolithic sac rather prominent, and projecting from the under surface of the ganglion.
- ". Hypopharyngeal band,' or gill and muscular system in every respect as in ordinary Salpw.
- "The arrangement of the zooids in this case very much resembles that in *Pyrosoma*, more especially the primary circle of the latter; but the whole economy in other respects is *Salpian*. Taken in the towing-net, lat. 32. 53 S., long. 156:00 E., and subsequently in other localities."

Orthocæla (Salpa pinnata of Authors).

It would be quite as philosophical to include the whole of the cheilostomatous Polyzoa under one generic term, as to group all the strikingly diversified animals of the Salpian type as mere species of the genus Salpa. Under a similar impression, Savigny set about the establishment of seven new genera; but their claims as such do not seem to be generally admitted by zoologists.

With regard to the genus here under consideration, I find the following observations amongst my notes:—

"While cruising in the S.W. Pacific, we frequently met with a Salpian answering perfectly to the description of Salpa pinnata, though this is rather indefinitely given by M. De Blainville; and in our late voyage to the West Indies in H.M.S. 'Icarus,' apparently the same species frequently made its appearance in the towing-net, together with Salpa zonaria, and numerous other species. It appears to me that the said S. pinnata, if I have correctly identified it, deserves to be removed from the genus Salpa, and placed by itself, until other species are added to it with the same generic characters. The propriety of this step, however, may be better seen when the principal features of the anatomy of the animal have been passed in review.

"In some instances specimens attain a length of about two inches, with a